Factors controlling *Eucalyptus* productivity: How water availability and stand structure alter production and carbon allocation

Michael G. Ryan [a,b,*], Jose Luiz Stape [c], Dan Binkley [d], Sebastiao Fonseca [e], Rodolfo A. Loos [e], Ernesto N. Takahashi [e], Claudio R. Silva [e], Sergio R. Silva [f], Rodrigo E. Hakamada [f], Jose Mario Ferreira [g], Augusto M.N. Lima [g], Jose Luiz Gava [h], Fernando P. Leite [i], Helder B. Andrade [j], Jacyr M. Alves [k], Gualter G.C. Silva [l]

[a] Rocky Mountain Research Station, USDA Forest Service, 240 W. Prospect, Fort Collins, CO 80526, USA
[b] Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA
[c] Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA
[d] Warner College of Natural Resources, Colorado State University, Fort Collins, CO 80523, USA
[e] Fibria Celulose, Aracruz, Espirito Santo, Brazil
[f] Veracel Celulose, Eunapolis, Bahia, Brazil
[g] International Paper, Mogi Guaçu, São Paulo, Brazil
[h] Suzano Papel e Celulose, Teixeira de Freitas, Bahia, Brazil
[i] CENIBRA, Ipatinga, Minas Gerais, Brazil
[j] Vallourec-Mannesmann, Bocaiuva, Minas Gerais, Brazil
[k] Copener Florestal, Alagoinhas, Bahia, Brazil
[l] Universidade Federal Rural do Semi-Árido, Mossoro, Rio Grande do Norte, Brazil

ARTICLE INFO

ABSTRACT

Wood production varies substantially with resource availability, and the variation in wood production can result from several mechanisms: increased photosynthesis, and changes in partitioning of photosynthesis to wood production, belowground flux, foliage production or respiration. An understanding of the mechanistic basis for patterns in wood production within a stand and across landscapes requires a complete annual carbon budget. We measured annual carbon flows to wood production, foliage production and total belowground carbon flux (the sum of root production, root respiration, and mycorrhizal production and respiration) from ages three to five years in clonal *Eucalyptus* plantations at four sites in Brazil to test if fertility, water availability and stand structure changed wood production and by what mechanism. We also quantified the patterns in light interception and the efficiency of light use to provide additional mechanistic insights into growth responses and to determine if light-use efficiency was related to changes in flux and partitioning.

The routine level of forest fertilization at these four sites was high enough that further increases in nutrient supply did not increase wood growth. Irrigation increased wood net primary productivity (age three to five) from 1.45 to 1.84 kg m^{-2} year^{-1} of C (27%), because of increases in light interception (5%), photosynthetic efficiency (from 0.028 to 0.031 mol C/mol photons absorbed, 11%), gross primary productivity (from 3.62 to 4.28 m^{-2} year^{-1} of C, 18%), and partitioning to wood (from 0.397 to 0.430 of photosynthesis, 8%). These changes increased light-use efficiency by 20%. Annual flux belowground varied among sites from 0.43 to 1.0 m^{-2} year^{-1} of C but did not vary with water availability. Across the four sites for the irrigated and unirrigated treatments, light-use efficiency was positively correlated with gross primary productivity and partitioning to wood production. Increasing heterogeneity of stand structure (resulting from staggered timing of planting within plots) led to a 14% loss in wood biomass relative to uniform stand structure at age six. Light-use efficiency, gross primary productivity, and wood net primary productivity were lower, but not significantly so, in heterogeneous compared to uniform stands.

Published by Elsevier B.V.

1. Introduction

The growth of wood in forests varies by more than a factor of two across local landscapes, and by more than 50% during the development of individual stands. The supply of resources

* Corresponding author at: USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect RD, Fort Collins, CO 80526-2098, USA.
Tel.: +1 970 498 1012; fax: +1 970 498 1010.
E-mail address: mgryan@fs.fed.us (M.G. Ryan).

(particularly water and nutrients) strongly influences wood production, but predicting how forest growth and ecosystem carbon storage respond to changes in resource supplies remains a challenge, particularly because the controls over carbon allocation are poorly understood (Landsberg, 2003; Trumbore, 2006). Considerable progress has been made for modeling the effects of climate and resources on wood production, and in some cases, other ecosystem carbon fluxes. However, lack of understanding of carbon allocation currently limits the capacity to model the forest carbon cycle, accurately predict the effects of global change on carbon cycling, and accurately predict forest productivity for new climates, sites and genotypes (Gower et al., 1997; Ryan et al., 1997; Friedlingstein et al., 1999; Landsberg, 2003; Litton et al., 2007).

Annual production per unit photosynthetically active light absorbed by the canopy (light-use efficiency, Monteith, 1972, 1977) provides simple, basic insights into changes in productivity and carbon allocation. The 'production' in light-use efficiency has been defined as crop or dry matter yield (Monteith, 1977), gross primary production or photosynthesis (for example, Drolet et al., 2005), and wood production (Linder, 1985), but we will use wood production in this paper. Differences in light-use efficiency indicate differences in canopy photosynthesis, partitioning of the annual photosynthesis to different sinks or respiration, or both.

Measuring canopy photosynthesis is very challenging, and the three methods commonly used (leaf measurements plus models, eddy covariance, carbon budget) have limitations. Photosynthesis can be estimated by measuring photosynthetic capacity of the canopy, the responses of photosynthesis and stomatal conductance to the environment, and using simple (for example, Landsberg and Waring, 1997) or complex models (for example, Williams et al., 2001; Medlyn, 2004) to extrapolate to the canopy. However this requires careful sampling that adequately represents the sources of variation within the canopy and through time. The limitations of this approach are the difficulty in obtaining the measurements in a tree canopy, spatial and temporal variability in photosynthetic capacity and the responses of photosynthesis and stomatal conductance to the environment, and the accuracy of any model used. A second way to estimate photosynthesis is to use net ecosystem exchange measurements from eddy covariance (Curtis et al., 2005; Sacks et al., 2007). Respiration at night is adjusted to temperatures during the day using a temperature response function, and added to the net ecosystem carbon exchange in the day. The strength of this approach is that it is derived from whole-canopy measurements. The limitations are that eddy covariance often underestimates ecosystem respiration because of advective flow and lack of turbulence (Lavigne et al., 1997), temperatures at night are rarely encountered during the day (at least in the same season), foliar respiration during the day is likely less than at night (Kirschbaum and Farquhar, 1984), and eddy covariance requires a large area with uniform vegetation (∼0.5 km^2), which makes assessing treatments and replication difficult. A third way to estimate photosynthesis is to measure the sinks and fluxes resulting from photosynthesis and sum them to get photosynthesis (Möller et al., 1954; Ryan, 1991). Estimation of total belowground carbon flux using soil respiration, litterfall, and carbon pool changes (Giardina and Ryan, 2002) has greatly aided this mass balance approach. The strengths of this approach are that it can be applied to small plots to assess treatment effects and that variability in respiration is lower than that for photosynthesis. The limitations are that much work is required to sample temporal and spatial variability and the accuracy of the models used to extrapolate measurements to the stand.

For this study, we used the third method of estimating photosynthesis, which has the additional advantage of providing estimates of the components of the carbon budget (Giardina et al., 2003; Maier et al., 2004; Ryan et al., 2004; Forrester et al., 2006;

Litton et al., 2007; Stape et al., 2008; Bown et al., 2009). We considered carbon flux for five major components: foliage respiration, foliage net primary production, wood respiration, wood net primary production, and total belowground carbon flux (carbon flux to root growth and respiration, exudates and mycorrhizae). We also manipulated resources (Linder, 1981; Raison and Myers, 1992) and assess how efficiency, and the three components of carbon allocation (biomass, flux, partitioning, Litton et al., 2007) change when resources and structure change. These manipulations were done over a six-year rotation (where final tree height reached ∼60% of the site maximum for the clone) for four locations with different climates for fast-growth *Eucalyptus* in Brazil. Our objectives were to measure changes in the C budget across sites to (1) increases in nutrient and water supply and (2) the uniformity of tree sizes within plots (stand structure). A third objective was to assess the importance of changes in flux, partitioning, light capture, and light-use efficiency in driving these responses.

2. Methods

2.1. Site descriptions

This paper reports data from four Brazil Eucalyptus Productivity Project (BEPP) sites, and these are described in detail in Stape et al. (2010). The Aracruz site was located at 19°49′S, 40°05′W near Aracruz City in Espirito Santo, Brazil on an Ultisol with a clay content of 37%. Mean annual temperature was 23.6 °C, with 1360 mm/year precipitation. Trees from the same clone were planted in March 2001 at a 3 m × 3 m spacing. The International Paper site was located 22°21′S, 46°58′W near Mogi Guaçu in São Paulo, Brazil on a oxisol with 45% clay content. Mean annual temperature through the rotation was 21.6 °C with 1320 mm/year precipitation. Trees were planted in October 2000 at a spacing of 3.0 m × 2.8 m. The Suzano site was located at 18°02′S, 39°52′W near Teixeira de Freitas in Bahia, Brazil on an Ultisol with 21% clay. Annual mean temperature was 23.1 °C, with 1350 mm/year precipitation. Trees were planted in December 2001 at 3 m × 3 m spacing. The Veracel site was located at 16°21′S, 39°34′W near Eunapolis in Bahia, Brazil on an Ultisol soil with about 37% clay content in the upper meter. Mean annual temperature during this rotation was 23.0 °C with an average of 1430 mm/year precipitation. Trees were planted in March 2001, at 3 m × 3 m spacing.

2.2. Experimental design

The Aracruz, Suzano, International Paper, and Veracel sites implemented two fertilization regimes, traditional (T) and non-limiting (F); irrigation to remove any soil water deficit (I) and unirrigated (N); and a uniform (U) or heterogeneous (H) stand structure. The traditional fertilizer regime represented current operational best practices for *Eucalyptus* and varied by site, based on current operations of each company. The non-limiting fertilization regime was applied quarterly throughout the study. For nutrients and amounts of fertilizer added, see Stape et al. (2010). For the irrigation treatment, water from a well or nearby stream was added weekly if needed to maintain soil water near field capacity. For the uniform treatment, trees from the same clone (but different clones among sites) were planted on the same day for each plot. For the heterogeneous treatment, one-third of the trees (again clonal) for a plot were planted, then one-third were planted 40 days after the first third, then the final third were planted 80 days after the first third. This scheme allowed the trees in the first third to establish dominance and led to a much more heterogeneous stand structure than the uniform treatment

([Binkley et al., 2010](#)). Aracruz, Suzano, International Paper, and Veracel each implemented four replicates of the FIU, FIH, FNU, and TNU treatments, but Aracruz measured the carbon budget only on one FIH and one FNU plot and two FNU and two TNU plots. The carbon budget was measured on all four replicate plots for the other three sites. Plots were ~30 m × 30 m, with a measurement plot of 36 trees (324 m²). Trenches were cut to 1 m deep around the irrigation and non-limiting fertilization plots to isolate them from adjacent plots. The carbon budget measurements were taken from ages two to five at the Aracruz and International Paper sites, and from ages three to five at the Suzano and Veracel sites.

We used a similar approach to estimating carbon fluxes and pools as outlined in [Ryan et al. (2004)](#) and [Stape et al. (2008)](#). We estimated wood production using quarterly diameter measurements and site-specific allometric equations; foliage production using quarterly diameter measurements and site-specific allometric equations and litterfall; total belowground carbon flux using a carbon balance approach ([Giardina and Ryan, 2002](#)) and measurements of litterfall, soil respiration, and changes in belowground carbon pools; and foliage and wood respiration using equations developed from *Eucalyptus* in Hawaii, adjusted for measurements at one site in Brazil ([Ryan et al., 2009](#)).

2.3. Biomass and aboveground net primary production

Biomass of stem, bark, branches, and roots >5 mm were estimated using allometric equations ([Table 1](#)). Equations were developed using trees harvested from all treatments over the life of the stand. Biomass by component was estimated using quarterly measurements of stem diameter at 1.3 m and tree height. We estimated net production of stems, branches, bark and roots >5 mm as the difference in biomass between two measurement periods. We estimated foliage net production as the difference in leaf biomass between two measurement periods plus any litterfall over the period. Based on data from [Stape et al. (2008)](#), we assumed dry mass was 45% carbon for stem and branch

wood, 48% carbon for foliage, and 42% carbon for roots >2 mm. Leaf area was estimated from leaf biomass and periodic samples of leaf mass per area.

2.4. Total belowground carbon flux

Total belowground carbon flux was estimated using techniques described in [Giardina and Ryan (2002)](#) and [Ryan et al. (2004)](#) as follows:

$$TBCF = F_S - F_A + \Delta(C_R + C_L + C_S + C_T) \tag{1}$$

where F_S is soil respiration, F_A is aboveground leaf and twig litterfall, C_R is root biomass, C_L is soil organic layer (forest floor) biomass, C_S is carbon in 0–0.45 m mineral soil, and C_T is the biomass in stumps and roots from the prior plantation (Aracruz and Suzano sites only). All stocks and fluxes were converted to carbon units.

Soil respiration was measured approximately monthly from ages three to five at all four sites and also at age two at the Aracruz and International Paper sites. Equipment breakdowns precluded monthly measurements for some months. At the Aracruz site, soil respiration was measured at nine locations per plot with a LI-COR 6400-09 soil efflux chamber (0.1 m diameter) using collars inserted into the soil 24 h prior to measurement. At the International Paper, Suzano, and Veracel sites, soil respiration was measured at nine locations per plot using a PP Systems EGM-4 gas analyzer with a PP Systems soil respiration chamber (0.1 m diameter). The PP Systems chamber was directly inserted into the soil without a collar for the measurements. The nine locations per plot were stratified into three strata: three samples were located in the planting rows, three midway between two planting rows and three one-quarter of the distance from the planting row centerline to the new planting row.

Because the PP Systems chamber can give higher efflux measurements when compared with the LI-COR 6400-09 chamber ([Janssens et al., 2000; Butnor et al., 2005](#)), we compared them once for each site where the PP Systems equipment was used. At the Aracruz site, we compared the Aracruz LI-6400-09 with the LI-6400-09 instrument used for the comparison with the other sites' PP Systems equipment at four plots. At the International Paper, Suzano, and Veracel sites, we measured soil CO_2 efflux with the LI-COR LI6400-09 and the PP Systems equipment used on site. Measurements were made 0.2 m apart in all plots with ongoing soil CO_2 efflux measurements. For the Aracruz site, the instruments gave a flux that differed overall by 0.14 μmol m^{-2} s^{-1} and a regression of the sample points gave $R^2 = 0.92$. At the International Paper site, a regression of the plot means gave LI-COR soil respiration = 0.83 × PP Systems soil respiration ($R^2 = 0.44$). For the Suzano site, a regression of the plot means for each instrument was not significant, but the mean difference of 1.68 μmol m^{-2} s^{-1} was. At the Veracel site, LI-COR soil respiration = 0.70 + 0.235 × PP Systems soil respiration ($R^2 = 0.28$). Because the LI-COR soil respiration instrument is likely to be more accurate, we used these equations or means to adjust the PP Systems measurements to that given by the LI-COR.

Previous studies had shown little or no diurnal variability in soil temperature and soil respiration for *Eucalyptus* in tropical locations ([Giardina and Ryan, 2002; Stape et al., 2008](#)), so we assumed no diurnal variability for these locations. Annual estimates of soil respiration were estimated using linear interpolation between sampling periods.

Litterfall was collected monthly in six 0.25 m² traps per plot, dried at 70 °C, and the branches >2 mm removed before weighing. Litter mass was corrected for decomposition prior to collection by adding decomposition losses (0.0072 per day, litter mass = collected mass × 1.1144) estimated from a litter

Table 1
Coefficients of the allometric equations by site and compartment. Equations are bole dry weight (kg) = aDBH^{b}H^c, where DBH is the diameter at breast height (cm), and H is the total height (m); branch or leaf dry weight (kg) = AGE^{a}DBH$^{b(b.AGE+c)}$, where AGE is the forest age (months) and DBH is the diameter at breast height (cm); coarse root (>5 mm diameter) dry weight (kg) = aW^b, where W is the bole biomass (kg). Trees were sampled at 12, 24 and 75 months of age for ARA, at 24 and 72 months of age for SUZ, at 12, 30, and 84 months of age for IPB, and at 12, 24, 64, 76 months of age for VER; n is sample size for each component.

Site	Bole	Branches	Leaves	Coarse Roots (>5 mm)
Aracruz—ARA				
a	0.004	−0.466	−1.807	0.3565
b	1.959	0.003	0.004	0.7773
c	1.512	1.349	2.713	
n	128	128	128	55
Suzano—SUZ				
a	0.009	−1.24	0.6278	2.3026
b	1.622	−0.008	3.0632	1.4988
c	1.515	3.002	−2.0283	
n	92	92	92	50
International Paper—IPB				
a	0.005	−1.445	−1.531	1.2279
b	1.751	0.00007	0.003	0.475
c	1.542	2.509	2.47	
n	169	169	169	61
Veracel—VER				
a	0.027	−1.163	−1.084	0.6691
b	2.221	0.004	−0.002	0.7858
c	0.625	2.063	2.084	
n	264	264	264	138

bag decomposition study at a similar site (Stape et al., 2008), and assuming litterfall was distributed uniformly through the collection period.

The organic soil layer (forest floor) was sampled annually at four 1 m^2 locations within each plot and a subsample was ashed in a muffle furnace to correct for any mineral soil in the samples. The annual change in forest floor was calculated from the mean difference per plot between these samples.

The 0–0.45 m mineral soil and soil bulk density was sampled at nine locations per plot and at three depths per location (0–0.15, 0.15–0.30 and 0.30–0.45 m) prior to plantation establishment and at harvest (age 6–6.5 years) at the same locations. The annual change in soil carbon was estimated as the per plot difference between these two samples divided by the time in years between the samples. The C content on the top 0.45 m of the soil profile represented 60% of the total C down to 2 m depth in a prior study (Stape et al., 2008). We expected the rate of change in soil C would be very small below 0.45 m depth relative to the upper soil, based on results from Bashkin and Binkley (1998). Soil C contents were converted to an area basis by plot by multiplying concentrations by average bulk density.

Stumps from the previous rotation comprised a substantial portion of soil carbon at the Aracruz and Suzano sites. We surveyed the old stumps in each plot after planting, measuring the diameter on the top of the stump. We used a regression from a prior study (Stape et al., 2008) to estimate initial stump and root biomass carbon. We estimated decomposition of the stumps and roots from the previous rotation assuming an exponential decay ($k = 0.190$ year^{-1}) measured in a previous study (Stape et al., 2008) and the stump and root biomass estimated above.

We estimated the change in root biomass (>5 mm) from site-specific allometric equations and diameter measurements. Ryan et al. (2004) found no change in fine root biomass after canopy closure and that fine root biomass (<2 mm diameter in their study) was less than 5% of the total root biomass for *Eucalyptus* in Hawaii. Therefore, we assumed no difference in fine root biomass important enough to impact the belowground carbon budget (fine root turnover was captured in soil respiration).

2.5. Light measurements

At the International Paper, Suzano, and Veracel sites, we measured light interception of photosynthetically active radiation every 3 months with a Decagon AccuPAR LP-80 Ceptometer (Decagon Devices, Pullman, WA, USA 99163) on three transects per plot with eight measurement locations each. Measurements were taken between 1030 and 1430 local time and compared with periodic clear sky readings to measure the light absorbed by the canopy. At the Aracruz site, we estimated light absorption from leaf area index measured with a LI-COR LAI-2000 (LI-COR Biosciences, Lincoln, NE, USA 68504) and an extinction coefficient for the exponential decay of light with leaf area estimated from destructive harvest measurements of leaf area made within a few days of the LAI-2000 measurements. We used linear interpolation to estimate light interception by the canopy for a year and calculated light-use efficiency from wood net primary production and canopy light absorption.

2.6. Aboveground tree respiration

Foliage respiration and wood CO_2 efflux were measured only for a two-week campaign at the Aracruz site (Ryan et al., 2009). At the Aracruz site, foliage dark respiration was identical to that found in fast-growth *Eucalyptus* in Hawaii (4.2 μmol C mol N^{-1} s^{-1} at 20 °C (Ryan et al., 2004)). We estimated foliar dark respiration for all sites using monthly estimates of leaf area and the mean flux per

unit leaf area measured at the Aracruz site for three- and four-and-a-half-year-old trees (0.66 μmol C m^{-2} s^{-1} at 20 °C). Rates were adjusted to the actual monthly mean temperature at night using an exponential relationship with temperature and a Q_{10} of 2. We applied the equation of Ågren and Axelsson (1980) to correct for the effect of temperature amplitude.

Wood CO_2 efflux at the Aracruz site (Ryan et al., 2009) was 8–10 times lower than that for similar sized trees for *Eucalyptus* in Hawaii (Ryan et al., 2004). Therefore, we estimated wood CO_2 efflux for all sites using the decline in CO_2 efflux with tree age and size in the Hawaii study (Ryan et al., 2009), with the average rates for wood CO_2 efflux measured for the three- and four-and-a-half-year-old trees (0.034 and 0.020 μmol (kg C)$^{-1}$ s^{-1} at 20 °C, respectively). Wood CO_2 efflux was estimated as follows:

Wood CO_2 efflux (mmol (kg C)$^{-1}$ s^{-1} at 20 °C)

$$= 0.25 \times \exp(-0.4949 \times \text{age (year)}) \qquad (2)$$

Rates were adjusted to the actual monthly mean temperature using an exponential relationship with temperature and a Q_{10} of 2. We applied the equation of Ågren and Axelsson (1980) to correct for the effect of temperature amplitude.

2.7. Statistical analysis

Because the sample design was unbalanced (for example, the heterogeneous treatment was only applied to the non-limiting, irrigation treatments), differences in fluxes and partitioning within a site were assessed using two-sample *t*-tests for the fertility, irrigation and stand structure treatments and the appropriate treatment pairs (FNU *versus* TNU for fertilization, FIU *versus* FIH for structure and FIU *versus* FNU for irrigation). Because rainfall and growth are highly variable among years, tests were applied to the means for ages three to five. The effect of operational fertilization versus non-limiting fertilization was also evaluated for aboveground wood biomass and aboveground wood net primary production using the mean of ages two through five. Differences in flux and partitioning with stand structure and irrigation across all sites were assessed using a paired samples *t*-test, with each site as a pair. Trends in flux, partitioning and light-use efficiency with gross primary productivity were assessed with linear regression. The Type I error level was $\alpha = 0.05$ with a 2-tailed test, even though our *a priori* predictions in some cases may have justified a less conservative use of a 1-tailed test. Analyses used SPSS Version 17.0 (SPSS Inc., Chicago, IL, USA 60606).

3. Results

3.1. Site productivity

Our four sites spanned a wide range in productivity and biomass at age six (Table 2). Wood biomass at age six varied from 5.6 kg m^{-2} of C (Suzano, TNU) to 11.1 kg m^{-2} of C (Veracel, FIU), wood net primary production at age three ranged from 0.83 m^{-2} year^{-1} of C (Aracruz, FNU) to 2.4 m^{-2} year^{-1} of C (Veracel, FIU), and gross primary productivity varied from 3.2 kg m^{-2} year^{-1} of C (Aracruz, FNU) to 5.5 m^{-2} year^{-1} of C (Veracel, FIU). Across all sites, wood NPP at age three was positively correlated with wood biomass at age six ($r = 0.89$).

3.2. Resource availability

Non-limiting fertilization increased wood production for only one of the four sites (Suzano, an 8% increase) compared to operational fertilization. The fertilization treatment had little or no effect on other fluxes or partitioning for the Suzano site or for the other sites.

Table 2
Stocks, fluxes, partitioning, and efficiency for unirrigated and irrigated treatments for *Eucalyptus* in Brazil. Means are averaged over stand ages three to five. Standard errors are calculated from the age three to five plot means.

|	Aracruz site				Suzano site				International Paper site				Veracel site			
	Unirrigated		Irrigated		Unirrigated		Irrigated		Unirrigated		Irrigated		Unirrigated		Irrigated	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Stocks (kg C m^{-2})																
Wood	3.01	0.45	5.00	0.75	3.80	0.48	4.66	0.60	3.91	0.46	4.78	0.59	5.56	0.65	6.76	0.62
Bole	2.60	0.43	4.50	0.73	3.26	0.55	4.00	0.69	3.69	0.47	4.51	0.60	5.21	0.64	6.34	0.61
Branch	0.41	0.01	0.50	0.03	0.54	0.07	0.67	0.10	0.22	0.01	0.27	0.01	0.35	0.02	0.42	0.01
Foliage	0.11	0.01	0.17	0.02	0.15	0.02	0.20	0.02	0.20	0.01	0.25	0.01	0.25	0.02	0.29	0.02
Roots > 5 mm	0.38	0.05	0.57	0.07	0.93	0.08	0.99	0.09	0.48	0.03	0.53	0.03	1.28	0.12	1.49	0.12
Fluxes (g m^{-2} year^{-1} of C)																
Wood	983	110	1,600	177	1,310	116	1,610	125	1,700	117	2,090	141	1,790	167	2,060	142
Bole	839	93	1,430	184	1,270	101	1,580	125	1,540	103	1,920	133	1,710	165	1,970	142
Branch	145	23	179	14	38	24	24	12	160	23	175	23	83	5	93	5
Foliage	176	26	218	33	205	39	240	71	254	9	278	6	216	24	232	20
ANPP	1,160	120	1,820	152	1,510	106	1,850	172	1,960	113	2,370	140	2,010	163	2,290	126
Foliage Respiration	330	24	416	41	429	25	491	31	491	20	544	15	584	52	588	49
Wood Respiration	493	34	829	133	678	82	821	61	859	38	1,060	51	925	98	1,070	105
Soil Respiration	1,240	282	1,250	288	1,280	124	1,340	109	768	46	811	54	705	35	665	34
Litterfall	318	41	377	50	292	22	345	48	402	27	434	33	294	20	317	18
Stump Biomass Change	−128	13	−128	13	−34	3	−34	3	0		0		0		0	
Root Biomass Change	88	7	133	23	183	32	191	20	91	7	101	7	311	30	347	32
Mineral Soil C Change	13	22	−70	34	−24	0	−24	0	−62	23	−50	35	−27	46	−3	32
Organic Soil C Change	99	85	124	85	28	3	13	6	28	25	29	23	32	15	32	19
Total Belowground C Flux	903	272	812	248	1,000	232	989	188	421	84	449	100	727	60	724	58
GPP	2,890	238	3,880	524	3,620	349	4,150	185	3,730	153	4,420	175	4,240	318	4,680	314
Partitioning (fraction)																
Foliage NPP:GPP	0.06	0.01	0.06	0.01	0.06	0.02	0.06	0.02	0.07	0.00	0.06	0.00	0.05	0.01	0.05	0.01
Wood NPP:GPP	0.35	0.05	0.42	0.02	0.36	0.03	0.39	0.03	0.46	0.02	0.47	0.02	0.42	0.01	0.44	0.01
Foliage Respiration:GPP	0.12	0.01	0.11	0.01	0.12	0.01	0.12	0.01	0.13	0.00	0.12	0.01	0.14	0.01	0.12	0.00
Wood Respiration:GPP	0.17	0.02	0.21	0.01	0.19	0.01	0.20	0.01	0.23	0.00	0.24	0.00	0.21	0.01	0.23	0.01
TBCF:GPP	0.30	0.07	0.20	0.04	0.27	0.05	0.24	0.04	0.11	0.02	0.10	0.02	0.17	0.01	0.16	0.01
Other																
LAI (m^2 m^{-2})	2.64	0.19	3.33	0.33	3.44	0.20	3.93	0.25	3.93	0.16	4.36	0.12	4.67	0.42	4.70	0.39
Leaf mass per area (kg/m^2)	0.101	0.001	0.101	0.001	0.116	0.004	0.116	0.004	0.108	0.001	0.108	0.001	0.110	0.001	0.110	0.001
APAR (MJ m^{-2} year^{-1})	1810	78	2050	106	2420	53	2520	52	2480	43	2580	32	2404	128	2424	122
Photosynthetic efficiency GPP/APAR (mol/mol)	0.028	0.002	0.033	0.003	0.028	0.002	0.029	0.001	0.026	0.001	0.030	0.001	0.031	0.002	0.033	0.001
Light-use efficiency (g C wood NPP MJ^{-1})	0.55	0.08	0.78	0.07	0.54	0.05	0.59	0.04	0.69	0.05	0.81	0.06	0.75	0.06	0.85	0.03
Growth efficiency (g C wood NPP LAI^{-1})	383	64	485	40	380	28	415	44	438	33	483	36	392	30	445	16
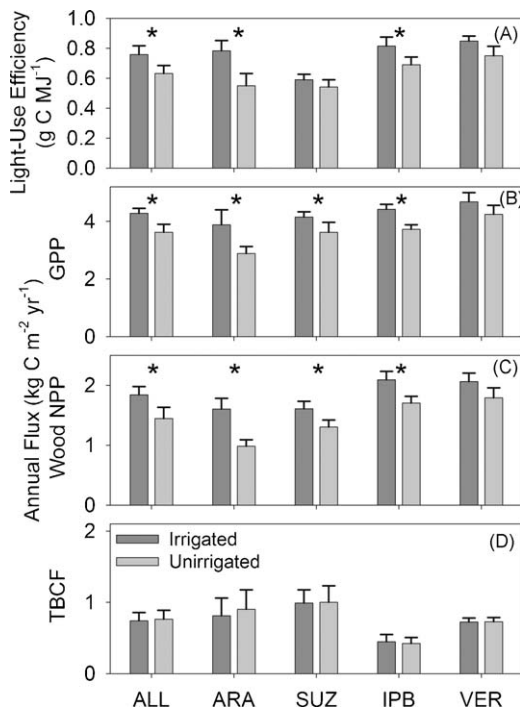
Fig. 1. Across all sites, irrigation increased (A) light-use efficiency (wood net primary productivity (NPP)/photosynthetically active radiation absorbed), (B) gross primary productivity (GPP), and (C) wood net primary productivity, but not (D) total belowground carbon flux (TBCF). Values are means for ages three to five. Error bars are standard errors for treatment means for each of the four sites, computed from the age three to five plot means. Pairs with a "*" were significantly different ($P < 0.05$).

Fig. 2. Wood net primary productivity (NPP) increases with (A) annual photosynthesis (GPP) via two mechanisms: higher carbohydrate supply (GPP) and (C) increased partitioning to wood NPP. Flux to TBCF (B) does not vary with GPP for these sites and treatments. Error bars are standard errors for treatment means for each of the four sites, computed from the age three to five plot means.

Across all sites, irrigation increased wood NPP by 27%, GPP by 18%, foliage production by 14% (Fig. 1), and GPP per unit of light absorbed by 10%. Total belowground carbon flux did not vary with water availability within or among sites (Fig. 1D). Fluxes to foliage production, wood CO_2 efflux, and foliage respiration all increased linearly as GPP increased across the site × irrigation gradient (r^2 = 0.46, 0.84, 0.91, respectively). Within a site, irrigation increased wood net production and GPP for all sites (Fig. 1), but the differences at the Veracel site were not significant (P = 0.08 and 0.09, respectively).

Flux to wood production increased through two mechanisms as water availability increased. First, greater photosynthesis provided more carbon for wood production (Fig. 2A). Higher photosynthesis resulted from an 11% increase in leaf area which yielded a 5% increase in absorbed photosynthetically active radiation. Photosynthesis per unit of light absorbed increased 13% in g C/APAR units, and from 0.028 to 0.032 mol C (mol photons)$^{-1}$ (11%). Second, the fraction of annual photosynthesis used for wood production also increased 8% as productivity increased (Fig. 2C). Irrigation did not affect the flux of carbon belowground for any of the sites, and belowground carbon flux was not related to annual photosynthesis (Fig. 2B). Increased productivity shifted partitioning between wood production and belowground, but only because of changes in the flux and partitioning of wood—flux belowground remained constant. Flux to foliage NPP, and foliage and wood respiration all increased with irrigation, but partitioning to those components was the same for irrigated and unirrigated stands.

3.3. Stand structure

Across all four sites, uniform stand structure for ages three to five increased wood NPP by 9% (P = 0.11) and GPP by 7% (P = 0.17, Fig. 3). These increases were not significant, but a significant difference in wood biomass (14%) at the end of the rotation (year 6)
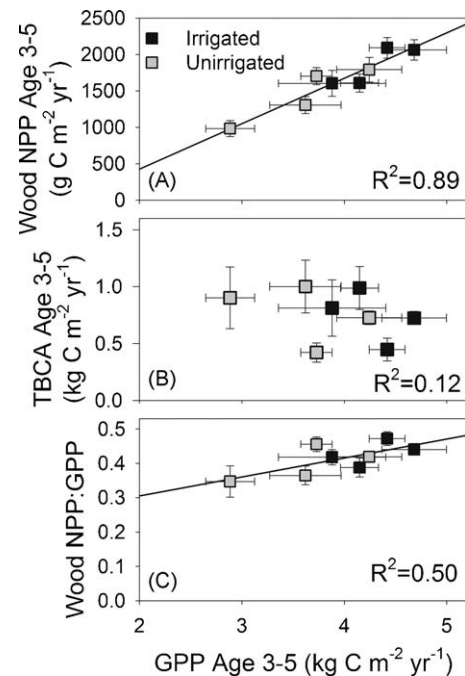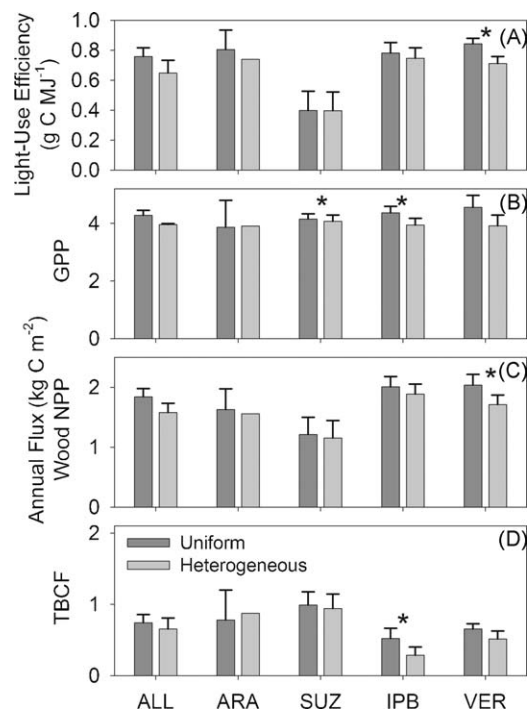

Fig. 3. The effect of stand structure (uniform—clonal individuals planted at the same time, heterogeneous, clonal individuals planted in three tranches separated by 40 days) on (A) light-use efficiency (wood net primary productivity (NPP)/photosynthetically active radiation absorbed), (B) gross primary productivity (GPP), (C) wood net primary productivity, and (D) total belowground carbon flux (TBCF). Averaged over all four sites, wood biomass at age six was 14% lower for the heterogeneous treatment. Error bars are standard errors for treatment means for each of the four sites, computed from the age three to five plot means. Pairs with a "*" were significantly different ($P < 0.05$).
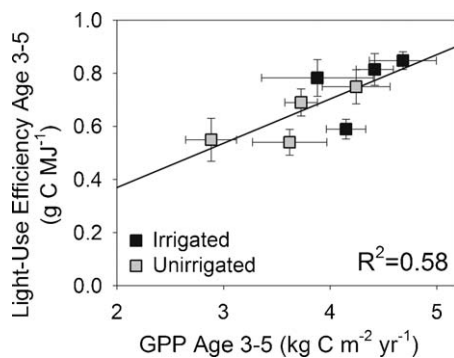
Fig. 4. Light-use efficiency (annual wood production per unit of photosynthetically active radiation absorbed) is positively correlated with mean gross primary productivity (GPP) for ages three to five. Error bars are standard errors for treatment means for each of the four sites, computed from the age three to five plot means.

indicated the effect of stand structure warrants confidence. Total belowground carbon flux did not vary much with stand structure across sites ($P = 0.33$). Stands with uniform structure had higher GPP for ages three to five for the Suzano and International Paper sites, higher light-use efficiency and wood NPP at the Veracel site, and higher total belowground carbon flux at the International Paper site (Fig. 3). Partitioning of annual photosynthesis at age five to wood production and belowground did not differ with stand structure.

3.4. Light-use efficiency

Light use and light-use efficiency were related to changes in flux and partitioning. Across sites, both wood net primary production (NPP) and gross primary productivity (GPP) increased with leaf area index ($R^2 = 0.84$ and 0.81, respectively) and with absorbed photosynthetically active radiation ($R^2 = 0.50$ and 0.53, respectively). Light-use efficiency for age three to five increased as gross primary productivity increased across sites or with irrigation (Fig. 4, $R^2 = 0.58$), primarily because partitioning and flux to wood production increased with GPP (Figs. 1 and 2). Across all sites, irrigation increased light-use efficiency by 20% (Fig. 1). Within sites, irrigation increased light-use efficiency at the Aracruz and International Paper sites, but the increases were not significant within the Suzano ($P = 0.06$) and Veracel sites ($P = 0.22$). Across all sites, uniform canopies had 9% greater light-use efficiency ($P = 0.12$), but the difference was not significant.

Contour plots illustrate how increases in growth were driven by increases in light use and efficiency of light use (Fig. 5). Over all sites (Fig. 5A), the 396 g C m^{-2} year^{-1} increase in wood production (27%) resulted from a 113 MJ m^{-2} year^{-1} increase in absorbed photosynthetically active radiation (APAR, 5%), a 0.2 g C/MJ increase in GPP/APAR (Fig. 5B, 13%), and a 0.033 fractional increase in the partitioning of GPP to wood NPP (8%). These changes yielded an increase in light-use efficiency of 0.13 g wood C/MJ APAR (20%).

4. Discussion

Increased supply of water increased both the carbohydrate available for wood growth (through increased photosynthesis), and the fraction of photosynthesis used for wood production. Both flux and partitioning appeared to be equally important. Across our site × irrigation productivity gradient, GPP increased 62% while wood NPP increased 114%. The greater percentage increase in wood NPP than GPP resulted from partitioning changing from 35% to 45% of GPP into wood NPP across the gradient in GPP. Fluxes to foliar respiration, wood CO_2 efflux, and foliage production efflux
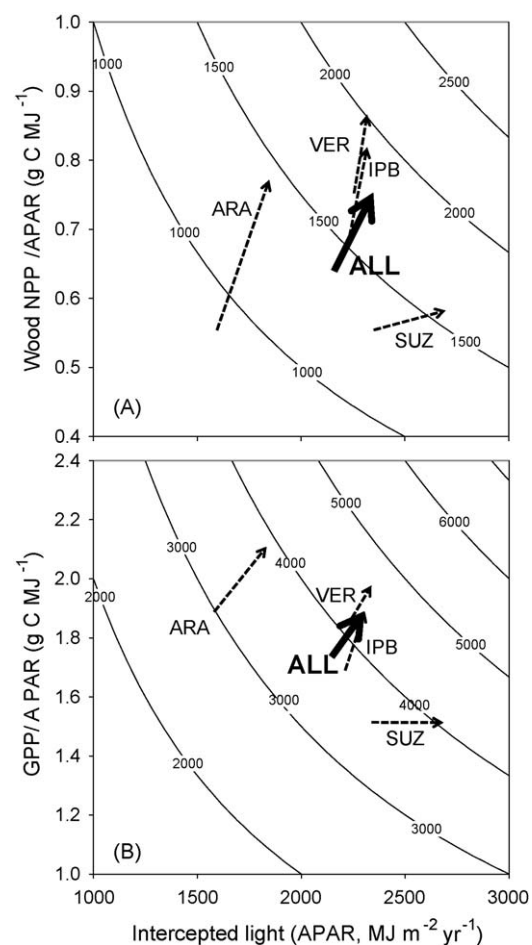

Fig. 5. The irrigation effect on (A) wood growth and (B) gross primary productivity (GPP) depended on changes in light capture (APAR) and efficiency of light use. These graphs show production as contour lines; horizontal vectors show the magnitude of the effect of increased APAR, and vertical vectors show the effect of increased light-use efficiency. The beginning of each arrow indicates the values for the unirrigated treatment, and the end of the arrow indicates the value for the irrigated treatment. The average vector across all sites angled at more than 45° from horizontal, indicating that gains in efficiency were more important than gains in APAR.

also increased as productivity increased, but partitioning changed less than 2% of photosynthesis.

With the exception of belowground flux, the patterns for flux and partitioning across the site × irrigation productivity gradient matched those found in Litton et al. (2007) in a cross-site study. Flux to wood NPP, respiration, and leaf production all increased as photosynthesis increased. Partitioning to wood production increased with GPP, while partitioning belowground decreased. Partitioning to wood CO_2 efflux, foliage respiration, and foliage production was constant over the BEPP productivity gradient, as also found in the Litton et al. (2007) study. The annual fraction of GPP used belowground and for wood production differed substantially between the BEPP study and the Litton et al. (2007) cross-site analysis. In the BEPP study, 42% of gross primary productivity went to wood production, compared to 30% for the cross-site analysis. And, in the BEPP study 19% of gross primary productivity went belowground, compared to 36% for the cross-site analysis. We suspect that tree-breeding efforts have changed partitioning to favor wood production relative to belowground flux for these fast-growth forests.

A remarkable result from these four studies is that belowground carbon flux did not change with increased water availability, contrary to our expectations from a cross-site study (Litton et al., 2007). Other studies have shown a broad range of changes in flux

and partitioning with changes in resource availability. Stape et al. (2008) found that irrigation increased GPP, wood NPP, and belowground flux by 10–13%, showing the irrigation effect was primarily on GPP with no shifts in partitioning. A fertility study in Hawaii (Ryan et al., 2004) found that increases in nutrient supply did not alter belowground flux, so the doubling of wood NPP indicated a major change in partitioning. Forrester et al. (2006) found that belowground carbon flux in a Eucalyptus–Acacia mixture was similar to that for pure-species stands, while aboveground primary productivity was greater in the mixed stand, also indicating a change in partitioning.

Belowground carbon flux was unchanged in an irrigation treatment, but decreased substantially in the irrigated plus fertilizer treatment in a study with radiata pine (Ryan et al., 1996). In that study, aboveground wood production increased by >100% for the irrigation plus fertilizer treatment compared to the control, while belowground flux decreased 28%. An irrigation and fertilization study in loblolly pine (Maier et al., 2004), found that belowground carbon flux increased 77% with fertilization and aboveground wood production increased 102%. A within and cross-site elevated CO_2 experiment (Palmroth et al., 2006) found that belowground flux decreased substantially as productivity increased (three angiosperm sites, one conifer site).

This sizable range of belowground responses in flux and partitioning to increases in resource supply show that no single pattern should be expected to apply generally, and that future work to explore the drivers of the variable responses of belowground flux and partitioning across experiments maybe very important. Predicting such site-specific responses will be particularly important for predicting the response of forest carbon storage to elevated CO_2 and nitrogen deposition (Ryan et al., 2008).

Belowground flux for this study varied twofold among site-clone combinations, from 0.43 m^{-2} year^{-1} of C at the International-al Paper site to 0.99 m^{-2} year^{-1} of C at the Suzano site. These fluxes are substantially lower than the ~1.8 m^{-2} year^{-1} of C measured for seed-grown Eucalyptus in Hawaii (Ryan et al., 2004), and the 1.4 m^{-2} year^{-1} of C measured for clonal Eucalyptus at another site in Brazil (Stape et al., 2008). We do not know the cause of the site or clone differences. Two potential candidates are differences among clones, or differences among sites in climate or soils. Climate for these four sites was similar for the study years (Stape et al., 2010), and belowground flux did not respond to irrigation, so we suspect climate is not the cause. Belowground flux did decrease as site clay content increased, suggesting a potential role for soil ($r^2 = 0.79$, $P = 0.11$, $n = 4$). We have no information on genetic differences in belowground flux, but the difference in flux between the seed-source Eucalyptus saligna in Hawaii and the clonal Eucalyptus urophylla X grandis hybrids in Brazil suggests that tree breeding may selected for genotypes with lower belowground flux.

Light-use efficiency was a good indicator of changes in the carbon balance. When fluxes or partitioning changed, efficiency did so as well, and the magnitude of the changes in efficiency, flux, and partitioning was similar. However, information on fluxes and partitioning was required to identify that both an increase in photosynthesis per unit of light absorbed and an increase in partitioning of photosynthesis to wood production increased wood production. The efficiency of photosynthesis was 0.031 mol C/mol photons for the irrigated treatments and 0.028 mol C/mol photons for the unirrigated treatments. This was lower than the 0.039 (unirrigated) and 0.052 (irrigated) - mol C/mol photons found in another Eucalyptus study in Brazil (Stape et al., 2008).

Wood growth across the site × irrigation gradient differed by 114%, and by 27% in response to irrigation alone. By taking a C budget approach, we gained insights into the mechanisms that explain these responses. For the site × irrigation gradient, leaf area index increased 78%, absorbed photosynthetically active radiation increased 34%, gross primary productivity increased 62%, and partitioning of photosynthesis to wood increased 27%. For the irrigation treatment averaged across sites, leaf area index increased 11%, absorbed photosynthetically active radiation increased 5%, photosynthetic efficiency (mol C photosynthesis per mole photosynthetically active radiation absorbed) increased 11%, gross primary productivity increased 18%, and partitioning of photosynthesis to wood increased 8%. These changes in flux and partitioning across the site × irrigation gradient or with irrigation alone increased light-use efficiency, and showed that detailed measurements are required to understand the mechanisms causing changes in light-use efficiency.

References

Ågren, G.I., Axelsson, B., 1980. Population respiration: a theoretical approach. Ecol. Model. 11, 39–54.

Bashkin, M.A., Binkley, D., 1998. Changes in soil carbon following afforestation in Hawaii. Ecology 79, 828–833.

Binkley, D., Stape, J.L., Bauerle, W.L., Ryan, M.G., 2010. Explaining growth of individual trees: light interception and efficiency of light use by Eucalyptus at four sites in Brazil. For. Ecol. Manage. 259, 1704–1713.

Bown, H.E., Watt, M.S., Clinton, P.W., Mason, E.G., Whitehead, D., 2009. The influence of N and P supply and genotype on carbon flux and partitioning in potted Pinus radiata plants. Tree Physiol. 29, 857–868.

Butnor, J.R., Johnsen, K.H., Maier, C.A., 2005. Soil properties differently influence estimates of soil CO_2 efflux from three chamber-based measurement systems. Biogeochemistry 73, 283–301.

Curtis, P.S., Vogel, C.S., Gough, C.M., Schmid, H.P., Su, H.B., Bovard, B.D., 2005. Respiratory carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999–2003. New Phytol. 167, 437–455.

Drolet, G.G., Huemmrich, K.F., Hall, F.G., Middleton, E.M., Black, T.A., Barr, A.G., Margolis, H.A., 2005. A MODIS-derived photochemical reflectance index to detect inter-annual variations in the photosynthetic light-use efficiency of a boreal deciduous forest. Remote Sens. Environ. 98, 212–224.

Forrester, D.I., Bauhus, J., Cowie, A.L., 2006. Carbon allocation in a mixed-species plantation of Eucalyptus globulus and Acacia mearnsii. For. Ecol. Manage. 233, 275–284.

Friedlingstein, P., Joel, G., Field, C.B., Fung, I.Y., 1999. Toward an allocation scheme for global terrestrial carbon models. Global Change Biol. 5, 755–770.

Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast growing Eucalyptus plantation estimated using a carbon balance approach. Ecosystems 5, 487–499.

Giardina, C.P., Ryan, M.G., Binkley, D., Fownes, J.H., 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Global Change Biol. 9, 1438–1450.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., Stow, T.K., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res.: Atmos. 102, 29029–29041.

Janssens, I.A., Kowalski, A.S., Longdoz, B., Ceulemans, R., 2000. Assessing forest soil CO_2 efflux: an in situ comparison of four techniques. Tree Physiol. 20, 23–32.

Kirschbaum, M.U.F., Farquhar, G.D., 1984. Temperature dependence of whole-leaf photosynthesis in Eucalyptus pauciflora Sieb. ex Spreng. Aust. J. Plant Physiol. 11, 519–538.

Landsberg, J., 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. Can. J. Forest Res. 33, 385–397.

Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecol Manage. 95, 209–228.

Lavigne, M.B., Ryan, M.G., Anderson, D.E., Baldocchi, D.D., Crill, P., Fitzjarrald, D.R., Goulden, M.L., Gower, S.T., Massheder, J.M., McCaughey, J.H., Rayment, M., Striegl, R.G., 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements. J. Geophys. Res. 102 (D24), 28977–28986.

Linder, S., 1981. Photosynthesis and respiration in a young stand of Scots pine. In: Proceedings of XVII IUFRO World Congress. International Union of Forestry Research Organizations, Japan, pp. 97–108.

Linder, S., 1985. Potential and actual production in Australian forest stands. In: Landsberg, J.J., Parsons, W. (Eds.), Research for Forest Management. CSIRO, Melbourne, Australia, pp. 11–35.

Litton, C.M., Ryan, M.G., Raich, J.W., 2007. Carbon allocation in forest ecosystems. Global Change Biol. 13, 2089–2109.

Maier, C.A., Albaugh, T.J., Allen, H.L., Dougherty, P.M., 2004. Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance. Global Change Biol. 10, 1335–1350.

Medlyn, B., 2004. A MAESTRO retrospective. In: Mencuccini, M., Grace, J., Moncrieff, J., McNaughton, K.G. (Eds.), Forests at the Land–Atmosphere Interface. CABI, Cambridge, MA, USA, pp. 105–121.

Möller, C.M., Müller, D., Nielsen, J., 1954. Graphic presentation of dry matter production in European beech. Det forstlige Forsögsväsen i Danmark 21, 327–335.

Monteith, J.L., 1972. Solar-radiation and productivity in tropical ecosystems. J. Appl. Ecol. 9, 747–766.

Monteith, J.L., 1977. Climate and efficiency of crop production in Britain. Philos. Trans. Roy. Soc. Lond. Ser. B: Biol. Sci. 281, 277–294.

Palmroth, S., Oren, R., McCarthy, H.R., Johnsen, K.H., Finzi, A.C., Butnor, J.R., Ryan, M.G., Schlesinger, W.H., 2006. Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO_2]—induced enhancement. Proc. Natl. Acad. Sci. 103, 19362–19367.

Raison, R.J., Myers, B.J., 1992. The biology of forest growth experiment: linking water and nitrogen availability to the growth of *Pinus radiata*. For. Ecol. Manage. 52, 279–308.

Ryan, M.G., 1991. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. Tree Physiol. 9, 255–266.

Ryan, M.G., Archer, S.R., Birdsey, R.A., Dahm, C.N., Heath, L.S., Hicke, J.A., Hollinger, D.Y., Huxman, T.E., Okin, G.S., Oren, R., Randerson, J.T., Schlesinger, W.H., 2008. Land resources. In: Janetos, T., Schimel, D., Backland, P. (Eds.), The Effects of Climate Change on Agriculture, Land Resources, Water Resources, and Biodiversity, SAP 4-3. US Climate Change Science Program, Washington, DC, USA, pp. 123–182.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., Senock, R.S., 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Monog. 74, 393–414.

Ryan, M.G., Cavaleri, M.A., Almeida, A.C., Penchel, R., Senock, R.S., Stape, J.L., 2009. Wood CO_2 efflux and foliar respiration for *Eucalyptus* in Hawaii and Brazil. Tree Physiol. 29, 1213–1222.

Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J., McMurtrie, R.E., 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nutrient status. Tree Physiol. 16, 333–343.

Ryan, M.G., Lavigne, M.B., Gower, S.T., 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. J. Geophys. Res. 102 (D24), 28871–28884.

Sacks, W.J., Schimel, D.S., Monson, R.K., 2007. Coupling between carbon cycling and climate in a high-elevation, subalpine forest: a model-data fusion analysis. Oecologia 151, 54–68.

Stape, J.L., Binkley, D., Ryan, M.G., 2008. Production and carbon allocation in a clonal *Eucalyptus* plantation with water and nutrient manipulations. Forest Ecol. Manage. 255, 920–930.

Stape, J.L., Binkley, D., Ryan, M.G., Fonseca, S., Loos, R., Takahashi, E.N., Silva, C.R., Silva, S., Hakamada, R.E., Ferreira, J.M., Lima, A.M., Gava, J.L., Leite, F.P., Silva, G., Andrade, H., Alves, J.M., 2010. The Brazil *Eucalyptus* Potential Productivity project: influence of water, nutrients and stand uniformity on wood production. Forest Ecol. Manage. 259, 1684–1694.

Trumbore, S., 2006. Carbon respired by terrestrial ecosystems - recent progress and challenges. Global Change Biol. 12, 141–153.

Williams, M., Bond, B.J., Ryan, M.G., 2001. Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. Plant. Cell. Environ. 24, 679–690.